

WATER AND TEMPERATURE RELATIONS OF THE PRIMITIVE  
XYLOPHAGOUS COCKROACH *CRYPTOCERCUS PUNCTULATUS*  
SCUDDER (DICTYOPTERA: CRYPTOCERCIDAE)

A. G. APPEL AND R. C. SPONSLER

Department of Entomology and Alabama Agricultural Experiment Station, Auburn University, Alabama 36849-5413.

---

*Abstract.*—Percent total body water content, cuticular permeability (CP), rate of water loss, and critical thermal maxima and minima were determined for the xylophagous cockroach *Cryptocercus punctulatus*. There was no difference between female and male *C. punctulatus* for any of the measured variables. Mean percent total body water was 75% and cuticular permeability was  $44.1 \mu\text{g cm}^{-2} \text{h}^{-1} \text{mm Hg}^{-1}$ . Critical thermal temperatures were  $40.3^\circ\text{C}$  and  $-7.8^\circ\text{C}$  for maxima and minima, respectively. The CP of *C. punctulatus* was similar to that of closely related blattid cockroaches and two sympatric termite species. Critical thermal temperatures were not similar to those of related taxa.

---

*Key Words:* Dictyoptera, *Cryptocercus punctulatus*, temperature sensitivity, water relations, desiccation

---

The primitive xylophagous cockroach, *Cryptocercus punctulatus* Scudder (Dictyoptera: Cryptocercidae), inhabits moist decaying hard and soft wood in the southern and northwestern United States. This species is considered an example of the close phylogenetic relationship between the cockroaches and termites (Cornwell 1968). Both groups have cellulose digesting gut protozoa and similar proventricular and genital morphology (McKittrick 1964). Within the Blattaria, *C. punctulatus* is most closely related to the Blattidae, the family that contains the pest genera *Blatta* and *Periplaneta*.

Not only do *C. punctulatus* consume wood, but they live in small social groups within wood. Colony galleries consist of networks of horizontal shafts, smaller transverse shafts, and enlarged arena-like areas (Nalepa 1984). The logs containing colonies

are quite damp, containing up to 80% moisture by weight (Appel pers. comm.). These cockroaches are primarily found in their galleries, but occasionally occur in the soil and leaf litter near decaying wood. Thus, *C. punctulatus* lives in a moist environment, buffered from rapid humidity and temperature changes.

The purpose of this study was to examine aspects of the water relations and temperature tolerance of *C. punctulatus* and to compare these parameters with those of closely related cockroaches and termites.

#### MATERIALS AND METHODS

Specimens of *C. punctulatus* were obtained 7 March 1987 and 12 January 1988 from decaying logs in Cleburne Co., Alabama, off U.S. 431, 2.8 km SE of the Cleburne-Calhoun Co. line (G. W. Folkerts,

Department of Zoology and Wildlife Science, Auburn University, pers. comm.). Adults, nymphs, and wood were returned to the laboratory for study.

**Water relations experiments.**—The water content, cuticular permeability (CP), and percent of total body water (% TBW) lost over time was determined gravimetrically with a digital balance (0.01 mg sensitivity) (Appel et al. 1983, Mack and Appel 1986). Percent TBW was calculated as the difference between the initial mass of live specimens and their mass after drying, divided by the initial live mass multiplied by 100. Dry mass was determined after the specimens were dried at ca. 50°C for at least three days or until two successive weighings did not differ >0.01 mg.

CP was calculated as the  $\mu\text{g}$  of water lost per unit surface area ( $\text{cm}^2$ ) per unit time (h) per unit saturation deficit (mm Hg) in a desiccator chamber. Individual cockroaches were placed in uncovered 30-ml plastic cups that were put into an 11-liter desiccator jar maintained at  $30 \pm 0.1^\circ\text{C}$  and 0–2% RH. The conditions in the desiccator were monitored with a Cole-Parmer LCD Digital Hygrometer (Model 3309-50). The hygrometer sensor was positioned at the same height in the desiccator as the specimens. Surface area was estimated for each specimen by Meeh's formula:  $S = 12 \cdot M^{2/3}$ , where  $S$  = surface area ( $\text{cm}^2$ ) and  $M$  = initial mass (g) (Edney and McFarlane 1974). Mass losses were measured at 2, 4, 6, 8, 10, and 24 h, but cuticular permeability was only calculated from 2 h-data. Preliminary experiments showed no significant difference in the amount of water lost by live and HCN-killed cockroaches at 2 h. Therefore, 2-h respiratory water was less than the sensitivity of the balance (0.01 mg) and cuticular permeability could be calculated from live cockroaches without complications of respiratory mass losses. Hourly mass loss and % TBW was used to calculate % TBW lost over time.

**Temperature relations experiments.**—Critical thermal maxima (CTMax) and

minima (CTMin) were defined as the upper or lower temperatures, respectively, that induced reversible knock-down when temperatures were rapidly increased (CTMax) or decreased (CTMin) at  $1^\circ\text{C}/\text{min}$  and 100% RH. Adult female and male *C. punctulatus* were used for CTMax and CTMin experiments. To determine CTMax, a 130-ml glass jar containing about 120 ml of water was sealed with a metal lid and placed into a 0.45-liter glass jar. A 5.5-cm-diameter plastic petri dish bottom containing a moistened disk of Whatman No. 2 filter paper was placed on top of the inner jar and 65 ml of water added to the space between the two jars. One cockroach was placed in the petri dish and the 0.45-liter jar was sealed with a metal lid and band. A small hole was cut in the center of the lid and a copper-constantan thermocouple (0.74-mm diameter) connected to a digital thermometer (Sensortek BAT-12) was threaded through the hole to contact the bottom of the petri dish. The thermocouple wire was attached to a 15-cm wooden applicator to ease manipulation. Body temperature and response to probing were determined by gently touching the thermocouple to the membrane between the cockroaches' meso- and metathoracic coxae. The jar-probe apparatus was placed on a hot plate that was adjusted to increase the temperature inside the apparatus at  $1^\circ\text{C}/\text{min}$ . Cockroaches were judged as knocked down when they lost coordination and the ability to right themselves. Recovery was assessed after 1 min at  $22.8^\circ\text{C}$ .

CTMin were measured in a covered 5.5-cm-diameter plastic petri dish containing a moistened disk of filter paper. A small hole was cut in the petri dish cover to allow access of the same thermocouple and probe as used for the CTMax determinations. A chill table was used as the cooling device and a constant rate of  $1^\circ\text{C}/\text{min}$  decline in temperature was maintained by varying the height of the petri dish above the chill table. Temperatures were measured as above, but

knock down was defined as the lack of leg movement when probed. Recovery was assessed after 15 min at 22.3°C. Leg movement was used in CTMin experiments because chilled cockroaches were not always immobilized on their dorsum as with CTMax.

**Statistical analysis.**—A completely randomized design and a Student's *t*-test (SAS Institute 1982) were used to determine significant differences in initial mass, % TBW, and cuticular permeability between sexes. Regression was used to determine if cuticular permeability was related to initial live mass or % TBW, and how % TBW loss was related to time. Data are expressed as means  $\pm$  SE. Completely randomized designs with sex as the factors were used for CTMax and CTMin. Student's *t*-tests ( $P \leq 0.05$ ) were used to determine significance. Data are expressed as means  $\pm$  SE.

## RESULTS AND DISCUSSION

Masses of *C. punctulatus* nymphs and adults ranged from 133.9 to 876.31 mg for second instars and adults, respectively. There was no difference between the masses of adult females ( $829.76 \pm 15.78$  mg) and males ( $781.83 \pm 17.93$  mg). All stages contained about 75% TBW and there was no difference between the % TBW of adult females and males (Table 1). Edney (1977) summarized the % TBW of a variety of arthropods (45–92% TBW) and Appel et al. (1983) reported a range of 62.7 to 71.8% TBW for ten cockroach species. The more primitive blattid species generally had greater % TBW than blattellid or blaberid species. Although the significance of % TBW is unknown, the close phylogenetic relationship of *C. punctulatus* with the blattids may relate to the similarity of % TBW among these species. In addition, the % TBW of two sympatric termite species, the Formosan subterranean termite, *Coptotermes formosanus* Shiraki and the eastern subterranean termite, *Reticulitermes flavipes* Koller (both Rhinotermitidae), ranged from 62.3

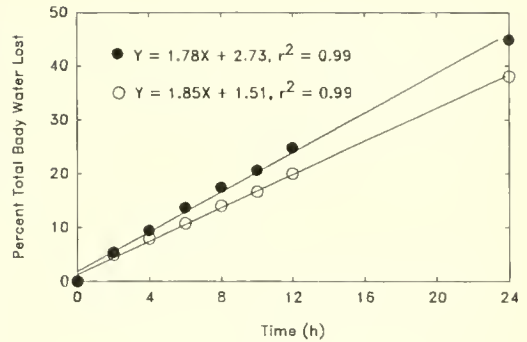


Fig. 1. Cumulative % TBW lost by female (○) and male (●) *Cryptocercus punctulatus* during desiccation at 30°C and 0–2% RH.

to 75.9 (Sponsler and Appel unpublished data).

Percent TBW loss of female ( $F = 32,502.1$ ,  $P = 0.0001$ ) and male ( $F = 2340.1$ ,  $P = 0.0001$ ) *C. punctulatus* increased linearly with desiccation time (Fig. 1). There was a significant difference between the rate of % TBW loss (slope  $\pm$  2 SE) of female and male *C. punctulatus*. This difference in rate probably resulted in the significant difference in 24-h mortality (Table 1). The greater mean mass of females, approximately 120 mg or 90 mg of water, accounts for the observed difference in desiccation-induced mortality. Linear rates of % TBW loss have been reported for cockroaches (Appel et al. 1983), termites (Sponsler and Appel unpublished data), and other insects (Mack and Appel 1986, Mack et al. 1988).

Cuticular permeability determines the rate of water loss. There was no relationship between the CP of female or male *C. punctulatus* and initial mass ( $F = 0.12$ ;  $df = 1$ ;  $P = 0.74$  and  $F = 0.00$ ;  $df = 1$ ;  $P = 0.99$ , respectively). Similarly, there was no relationship between CP and % TBW for males ( $F = 1.92$ ;  $df = 1$ ;  $P = 0.20$ ). The CP of females, however, declined linearly ( $F = 6.47$ ;  $df = 1$ ;  $P = 0.03$ ) with % TBW (CP =  $-0.91$  % TBW + 111.69;  $r^2 = 0.45$ ). Appel et al. (1986) found that water loss of adult male *Periplaneta fuliginosa* (Serville) was

Table 1. Initial masses, percent total body water (% TBW), cuticula permeability, and mortality of female and male *C. punctulatus* [ $\bar{x} \pm SE$ ; n = 20].

Sex	Initial Mass (mg)	% TBW	Cuticular Permeability <sup>a</sup>	Mortality at 24 h
Female	596.69 $\pm$ 78.20	74.87 $\pm$ 1.39	43.52 $\pm$ 1.89	30%
Male	476.11 $\pm$ 67.70	76.01 $\pm$ 0.66	44.73 $\pm$ 3.25	90%

<sup>a</sup>  $\mu\text{g cm}^{-2} \text{h}^{-1} \text{mm Hg}^{-1}$ .

negatively related to body lipid content. The negative relationship observed with female *C. punctulatus* may also be related to lipid content and factors such as age and reproductive status that affect lipid content.

There was no difference between the CP of female and male *C. punctulatus* (Table 1). The CP of *C. punctulatus* ( $44.1 \mu\text{g cm}^{-2} \text{h}^{-1} \text{mm Hg}^{-1}$ ) was similar to those of blattid cockroaches such as *Periplaneta americana* (L.), *Periplaneta australasiae* (Fab.), *Blatta orientalis* (L.), and *Periplaneta brunnea* Burmeister with CP values of 53.7, 43.1, 43.4, and  $41.7 \mu\text{g cm}^{-2} \text{h}^{-1} \text{mm Hg}^{-1}$ , respectively (Appel et al. 1983). The CPs of worker *C. formosanus* and *R. flavipes* were also similar to *C. punctulatus* (37.5 and  $27.8 \mu\text{g cm}^{-2} \text{h}^{-1} \text{mm Hg}^{-1}$ , respectively) (Sponsler and Appel unpublished data). Arthropods with CPs of approximately 40 generally inhabit hygric environments such as tropical forests, moist wood, and sewers (Edney 1977).

Even though the CPs of female and male *C. punctulatus* were not different, the rates of % TBW loss (see above) were significantly different. Differences in initial mass explain this apparent discrepancy. Although both sexes had the same CP ( $44.1 \mu\text{g cm}^{-2} \text{h}^{-1} \text{mm Hg}^{-1}$ ), there was significantly more water in females than in males. Therefore, females lose a lower percentage of their % TBW than males at any given time.

There was no difference between the critical thermal temperatures of female and male *C. punctulatus*. Critical thermal temperatures ranged from 40.9 to  $-8.5^\circ\text{C}$  for CTMax and CTMin, respectively (Table 2). The CTMax of *C. punctulatus* is the lowest recorded for cockroaches. Previously reported cockroach CTMax ranged from 47.6 to  $51.4^\circ\text{C}$  (Appel et al. 1983); the CTMax of *C. punctulatus* was nearly  $7.5^\circ\text{C}$  lower than that of the next lowest cockroach species. Positive correlations between CTMax and habitat temperatures have been established for desert cockroaches (Cohen and Pinto 1977, Cohen and Cohen 1981), desert termites (Rust et al. 1979), and meloid beetles (Cohen and Pinto 1977). Appel et al. (1983) found that the CTMax of ten cockroach species, representing three families, could be divided into four statistically distinct groups:  $<48.1^\circ\text{C}$ ,  $48.7\text{--}49.1^\circ\text{C}$ ,  $49.3\text{--}49.5^\circ\text{C}$ , and  $>49.6^\circ\text{C}$ . There was no apparent phylogenetic relationship in the ability to tolerate high temperatures, and our results with *C. punctulatus* support this conclusion.

Few studies have reported the CTMin of insects. Sponsler and Appel (unpublished data) determined the CTMin for soldier and worker *C. formosanus* and *R. flavipes*. The mean CTMin for these termites was  $13.2^\circ\text{C}$  and there was no difference between stages or species. Although collected at the same time of year as these termites, the CTMin

Table 2. Critical thermal temperatures ( $^\circ\text{C}$ ) of adult *C. punctulatus* [ $\bar{x} \pm SE$  (minimum–maximum); n = 10].

Sex	CTMax	CTMin
Female	39.6 $\pm$ 0.28 (39.0–40.5)	$-8.5 \pm 0.52$ ( $-10.0\text{--}-7.2$ )
Male	40.9 $\pm$ 0.21 (39.7–40.9)	$-7.1 \pm 0.55$ ( $-9.0\text{--}-7.1$ )

of *C. punctulatus* ranged from  $-10.0$  to  $-7.1^{\circ}\text{C}$ . In addition, *C. punctulatus* remain active at  $-5.0$  to  $0^{\circ}\text{C}$  (Appel unpublished data). Preliminary studies with *P. americana* and *B. orientalis* indicated that the CTMin of these cockroaches was much higher (ca.  $10^{\circ}\text{C}$ ) than that of *C. punctulatus*.

Differences in temperature tolerance between *C. punctulatus* and sympatric termites are likely due to differences in microhabitats. *Cryptocercus punctulatus* live in moist, fallen, partially buried logs in dense forests (Seelinger and Seelinger 1983, Nalepa 1984). These logs provide a habitat insulated by moisture. With leaf littered soil as a heat-sink, these logs maintain lower than ambient temperatures (Appel unpublished data). During hot spells, evaporation cools the logs. It is also possible that the cockroaches move to preferred cooler locations within their extensive galleries. Rhinotermitid termites, however, usually maintain soil contact even when they forage on surface debris. Since most colonies are located well below the soil surface (and frost line) and are composed of thousands of metabolically active individuals, these termites are probably exposed to more constant, warm temperatures than are log inhabiting *C. punctulatus*.

Similar CPs among *C. punctulatus*, blattid cockroaches, and termites may reflect their similar high-humidity habitats or close phylogenetic relationships. The interstitial spaces in wood or soil containing  $>17\%$  moisture are at saturated humidity and do not contribute to significant body water loss. Since all of these groups inhabit moist areas, it is not surprising that they all have similar CPs. Our results concur with the conclusions of Appel et al. (1983) that, in cockroaches, CP is related to habitat moisture and temperature sensitivity is related to habitat temperature.

#### ACKNOWLEDGMENTS

We thank George W. Folkerts, Department of Zoology and Wildlife Science, Au-

burn University, for collecting the *C. punctulatus* and for reviewing the manuscript. Alabama Agricultural Experiment Station Journal Series No. 17-881834P.

#### LITERATURE CITED

- Appel, A. G., D. A. Reiersen, and M. K. Rust. 1983. Comparative water relations and temperature sensitivity of cockroaches. *Comp. Biochem. Physiol.* 74A: 357-361.
- . 1986. Water relations of the smokybrown cockroach, *Periplaneta fuliginosa*. *J. Insect. Physiol.* 32: 623-628.
- Cohen, A. C. and J. L. Cohen. 1981. Microclimate temperature and water relations of two species of desert cockroach. *Comp. Biochem. Physiol.* 69A: 165-167.
- Cohen, A. C. and J. D. Pinto. 1977. An evaluation of xeric adaptiveness of several species of blister beetles (Meloidae). *Ann. Entomol. Soc. Am.* 70: 741-749.
- Cornwell, P. B. 1968. *The Cockroach*, Volume I. Hutchinson & Co. LTD, London. 391 pp.
- Edney, E. B. 1977. *Water Balance in Land Arthropods*. Springer, New York. 282 pp.
- Edney, E. B. and J. McFarlane. 1974. The effects of temperature on transpiration in the desert cockroach, *Arenivaga investigata* and in *Periplaneta americana*. *Physiol. Zool.* 47: 1-12.
- Mack, T. P. and A. G. Appel. 1986. Water relations of immature and adult lesser cornstalk borers, *Elasmopalpus lignosellus* (Lepidoptera: Pyralidae). *Ann. Entomol. Soc. Am.* 79: 579-582.
- Mack, T. P., A. G. Appel, C. B. Backman, and P. J. Trichilo. 1988. Water relations of several arthropod predators in the peanut agroecosystem. *Environ. Entomol.* 17: 778-781.
- McKittrick, F. A. 1964. Evolutionary studies of cockroaches. *Cornell Univ. Agric. Exp. Sta. Mem.* 389: 1-197.
- Nalepa, C. A. 1984. Colony composition, protozoan transfer and some life history characteristics of the woodroach *Cryptocercus punctulatus* Scudder (Dictyoptera: Cryptocercidae). *Behav. Ecol. Sociobiol.* 14: 273-279.
- Rust, M. K., D. A. Reiersen, and R. H. Scheffrahn. 1979. Comparative habits, host utilization and xeric adaptations of the southwest drywood termites, *Incisitermes fruticavus* Rust and *Incisitermes minor* (Hagen) (Isoptera: Kalotermitidae). *Sociobiology* 4: 239-255.
- SAS Institute. 1982. SAS user's guide: Statistics. SAS Institute, Cary, N.C.
- Seelinger, G. and U. Seelinger. 1983. On the social organisation, alarm and fighting in the primitive cockroach *Cryptocercus punctulatus* Scudder. *Z. Tierpsychol.* 61: 315-333.